A mass-balanced Ecopath model of Great Slave Lake to support an ecosystem approach to fisheries management : Preliminary Results

M. Y. Janjua and R. F. Tallman

Arctic Aquatic Research Division
Central and Arctic Region
Fisheries and Oceans Canada
501 University Crescent
Winnipeg, MB R3T 2N6

2015

Canadian Technical Report of
Fisheries and Aquatic Sciences 3138

Fisheries and Oceans Canada | Pêches et Océans Canada

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques*.

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of
Fisheries and Aquatic Sciences 3138

2015

A MASS-BALANCED ECOPATH MODEL OF GREAT SLAVE LAKE TO SUPPORT AN ECOSYSTEM APPROACH TO FISHERIES MANAGEMENT : PRELIMINARY RESULTS

by

M. Y. Janjua and R. F. Tallman

Central and Arctic Region
Fisheries and Oceans Canada
501 University Crescent
Winnipeg, MB, R3T 2N6

© Her Majesty the Queen in Right of Canada, 2015.

Cat. No. Fs97-6/3138E-PDF ISBN 978-0-660-03206-4 ISSN 1488-5379

Correct citation for this publication is:

Janjua, M.Y. and Tallman R.F. 2015. A mass-balanced Ecopath model of Great Slave Lake to support an ecosystem approach to fisheries management : Preliminary Results. Can. Tec. Rep. Fish. Aquat. Sci. 3138: vi + 32 p.

TABLE OF CONTENTS

TABLE OF CONTENTS	iii
LIST OF TABLES	iv
LIST OF FIGURES	iv
ABSTRACT	v
RÉSUMÉ	vi
1. INTRODUCTION	1
1.1- Site Description	1
1.2- Fisheries Management	2
2. CLIMATE CHANGE IMPACTS ON GREAT SLAVE LAKE	3
3. MODELLING FRAMEWORK	4
4. MODEL PARAMETERIZATION	5
4.1- Functional Groups	6
4.2- Primary Production	6
4.3- Fish	6
4.4- Invertebrate Fauna	7
4.5- Detritus	7
4.6- Harvest Data	8
4.7- Balancing the Model	8
4.8- Model Valuation	8
5. TROPHIC NETWORK ANALYSIS	8
5.1- Flows and Biomasses	9
5.2- Ecosystem Indices and Attributes	9
5.3- Mixed Trophic Impact and Keystoneness	11
5.4- Primary Production Required (PPR)	12
6. MODEL SIMULATIONS	12
6.1- Preliminary Fisheries Simulations	12
6.2- Climate Change Simulations	13
7. FUTURE WORK AND CONCLUSION	13
8. REFERENCES	14

LIST OF TABLES

Table1. List of functional groups and data source for Great Slave Lake Ecopath model 22

Table 2. Balanced parameter estimates for the Great Slave Lake Ecopath model. 24

Table 3. Balanced diet matrix for the Great Slave Lake ecosystem Ecopath model showing proportions of each prey in the diet of predators. 25

Table 4. Trophic transfer matrix of the Great Slave Lake ecosystem Ecopath model showing the distribution of absolute flows ($t.km^{-2}.yr^{-1}$) by groups and trophic levels. 26

Table 5. Transfer efficiency at various TLs showing the contribution of detritus and primary production to the Great Slave Lake trophic network. 26

Table 6. A summary of metrics and indices for structural properties of Great Slave Lake ecosystem 27

Table 7. Totals of flux indices for the Great Slave Lake ecosystem model. 27

Table 8. Primary Production Required (PPR) for consumption and harvest of functional groups in the Great Slave Lake ecosystem 28

LIST OF FIGURES

Figure 1. Map of Great Slave Lake showing the management areas and areas closed to commercial fishing. 29

Figure 2. Pedigree index of data used for the Great Slave Lake Ecopath model. Colors in the legend describe the data origin and quality. 29

Figure 3. The Ecopath outputs based on the Great Slave Lake food web conceptualization. 30

Figure 4. Lindeman spine of the Great Slave Lake ecosystem showing aggregation of flows into a concatenated chain of transfers through tropl ic levels. 30

Figure 5. Mixed trophic impact of the Great Slave Lake ecosystem. 31

Figure 5. Keystoneness of different functional groups in Great Slave Lake. 31

Figure 5. Predicted relative change in biomass of fished species in Great Slave Lake in 20-years period by reducing the fishing effort to 25%. 32

Figure 5. The relative change in biomass of functional groups in the Great Slave Lake ecosystem after imposing a -15% to +15% changes in the primary production over a 50-year period. 32

ABSTRACT

Janjua, M.Y. and Tallman R.F. 2015. A mass-balanced Ecopath model of Great Slave Lake to support an ecosystem approach to fisheries management : Preliminary Results. Can. Tec. Rep. Fish. Aquat. Sci. 3138: vi + 32 p.

We have described the sub-Arctic Great Slave Lake (GSL) ecosystem using a mass-balance model to understand trophic interactions, sustainability of fisheries and ecosystem health. Model is composed of 19 functional groups including thirteen fish groups and four invertebrates groups. In terms of biomass, lake whitefish followed by cisco and sucker dominated the ecosystem. Burbot was found to be the main keystone species, having a relatively higher impact. The study showed that the GSL fisheries required 3.13 % of the total primary production, a small proportion of the productive capacity of the ecosystem. Moderate trophic level of catch (3.24) and the low percentage of primary production required, indicated that the fishery during the modeling period was in a sustainable range. The relative ascendancy for Great Slave Lake was lower than Lake Superior and Lake Ontario, which was an indication of its ecosystem maturity and stability. The internal redundancy was also high, an indication that this ecosystem possessed significant reserves to overcome substantial external disturbances. We simulated a fishing scenario over a 20 year period by reducing the overall fishing effort to 25% and observed changes in relative biomass trajectories of fish functional groups. With default vulnerabilities, lake trout showed a 50% and inconnu showed a 28% initial increase in relative biomass. Results of Ecosim simulations showed that the key resources, like the lake whitefish fisheries was quite sustainable, however, lake trout and inconnu were likely to show a rapid decline with an increase in fishing effort and pressure. We did some preliminary simulations using the Ecosim linear forcing function on the rate of primary production to specify a temporal increase and decrease in the percent primary production over 50-year periods. The largest change was observed in the whitefish biomass and minimum change was recorded for walleye and lake trout. Our model provides a base that can be upgraded as new information becomes available. Further research on the diversity, productivity, growth, and biomass of different functional groups in the GSL ecosystem is ongoing: results will be helpful in improving this model by the addition of more data.

RÉSUMÉ

Janjua, M.Y., et Tallman, R.F. 2015. A mass-balanced Ecopath model of Great Slave Lake to support an ecosystem approach to fisheries management: Preliminary Results. Rapp. tech. can. sci. halieut. aquat. 3138: vi + 32 p.

Nous avons décrit l'écosystème subarctique du Grand lac des Esclaves (GLE) à l'aide d'un modèle équilibré en fonction de la masse afin de comprendre les interactions trophiques, la durabilité des pêches et la santé de l'écosystème. Le modèle est composé de dix-neuf groupes fonctionnels, dont treize groupes de poissons et quatre groupes d'invertébrés. Sur le plan de la biomasse, le grand corégone, suivi du cisco et du meunier, dominait l'écosystème. La lotte était la principale espèce clé, car elle avait une incidence relativement plus grande. L'étude a montré que les pêches dans le GLE exigeaient 3,13 % du total de la production primaire, soit une petite proportion de la capacité de production de l'écosystème. Un niveau trophique modéré des prises (3,24) et le faible pourcentage de la production primaire requis indiquaient que la pêche, au cours de la période de modélisation, se situait dans la fourchette de durabilité. La valeur relative ascendante du GLE était plus faible que celle du lac Supérieur et du lac Ontario, ce qui démontre la maturité et la stabilité de l'écosystème. La redondance interne était aussi élevée, ce qui indique que cet écosystème peut compter sur de grandes réserves lui permettant de surmonter d'importantes perturbations d'origine externe. Nous avons simulé un scénario de pêche sur 20 ans en réduisant l'effort de pêche général à 25 %, et observé des changements dans les trajectoires de la biomasse relative des groupes fonctionnels de poissons. Compte tenu des vulnérabilités par défaut, le touladi a affiché une réduction de 50 % et l'inconnu, une hausse initiale de 28 % de la biomasse relative. Les résultats des simulations avec Ecosim ont démontré que les ressources clés, comme la pêche au grand corégone, ont été très durables. Toutefois, le touladi et l'inconnu étaient susceptibles d'afficher un déclin rapide en cas d'augmentation des efforts et de la pression de la pêche. Nous avons effectué des simulations préliminaires à l'aide de la fonction de contrainte linéaire dans Ecosim sur le taux de production primaire afin de préciser une augmentation et une diminution temporelles de la production primaire en pourcentage au cours d'une période de récurrence de 50 ans. Le changement le plus important a été observé dans la biomasse minimale du grand corégone, et le plus faible changement a été enregistré pour le doré jaune et le touladi. Notre modèle fournit une base qui peut être mise à jour à mesure que de nouveaux renseignements deviennent disponibles. D'autres recherches sur la diversité, la productivité, la croissance et la biomasse de différents groupes fonctionnels dans l'écosystème du GLE sont en cours : les résultats seront utiles pour améliorer ce modèle par l'ajout d'une plus grande quantité de données.

1- INTRODUCTION

Fishing and environmental changes influence the structure and function of ecosystems. It is important to determine the relative importance of these controlling forces by the development of ecosystem models that can be used to explore ecosystem response to these changes. Ecosystem models can be used as a tool to identify potential changes in complex ecosystems including the impacts of fishing or climate change. How climate change could affect the structure of an ecosystem depends not only on the species being affected but also on the structure and functioning of the ecosystem (Shannon et al. 2009). According to Cury et al. (2008), effects of climate-driven productivity changes in ecosystems and fisheries can be explored by the use of food web modelling. The Ecopath with Ecosim (EwE) software (Christensen et al. 2008) is the most relative and used ecosystem modelling tool to study ecosystem-level responses to changes in fishing and climate influence. Zhang et al. (2011) has proposed an Integrated Fisheries Risk Analysis Method for Ecosystems (IFRAME) framework for evaluating the performance of management strategies relative to the goals of an ecosystem approach to management (EAM) under different climate change scenarios and for the assessment of ecosystem impacts of resource use and climate change in marine ecosystems. The IFRAME approach tracks climate change impacts on the flow of energy through the planktonic food web (Kishi *et al.*, 2007) and projects the implications of these shifts in bottom-up forcing on the fisheries food web using Ecopath with Ecosim.

Ecopath with Ecosim models have been developed for many Canadian marine and Great Lakes ecosystems but no such model has been developed for the large freshwater ecosystems in the Canadian Arctic and sub-Arctic. We describe the sub-Arctic Great Slave Lake (GSL) ecosystem using a mass-balance model to understand trophic interactions, sustainability and ecosystem health. The objective of this report is to describe the EwE model of the GSL ecosystem including data sources, model parameterisation, functional groups, data gaps, trophic interactions, and ecological network analysis to describe the ecosystem attributes and results of few preliminary simulations to understand the impact of fisheries and climate change. This work is a part of the Northwest Territories Cumulative Impact Monitoring Program (NWT CIMP) and Aquatic Climate Change Adaptation Services Program (ACCASP),

1.1- SITE DESCRIPTION

Great Slave Lake located between Great Bear Lake and Lake Athabasca is one of three great lakes in the Mackenzie River Basin. It is the second-largest lake in the Northwest Territories of Canada and the ninth largest lake in the world. It is a deep, oligotrophic lake and falls within two physiographic regions, the Precambrian Shield and the Interior Plains or lowlands (Kang et al. 2012). GSL has a surface area of 28,568 km^2 with a total volume of 1070 km^3, a mean depth of 41 m and a maximum depth of 614 m (Rawson 1950, Herdendorf 1982). It is 480 km long and 19 to 109 km wide. It is the deepest lake in the North America. The lake basin is divided into two regions, the West Basin which is relatively shallow with mean depth of 41 m and the East Arm which is substantially deeper with Christie Bay having a mean depth 199 m and McLeod Bay having a mean depth of 120 m. The Canadian Shield divides GSL. The West Basin is located on Paleozoic deposits while the East Arm is on the Precambrian Shield.

Lockhart, Yellowknife, Snare and several smaller rivers are in north and east part but provide very little discharge. The area to the south and west of the Precambrian dividing line is known as the Mackenzie lowlands. This is the Northern border of the Great Plains and includes a major portion of the GSL central area. The Slave River is the major water source contributing almost 87% of the water along with large quantities of sediments. Other important tributaries in the south are Hay River and Buffalo River. GSL has a very large drainage basin (983,000 km^2). Water flows north from GSL through the Mackenzie River. GSL has a residence time of 16 years based on the total lake volume and seven years based on the volume of the West Basin (Evans 2000). It functions as a hydrologic, biogeochemical and sedimentary regulator for almost 50% of the annual basin runoff to the Arctic Ocean (Gibson et al. 2006).

The main lake basin is exceptionally productive given its northerly latitude (Fee et al. 1985). This productivity may be due to high nutrient and particulate organic matter inputs originating from the Slave River (Evans 2000). The lake is relatively unpolluted and there has not been any introduction of non-native species. Chrysophytes, cryptophytes and diatoms form the bulk of the phytoplankton production in the lake (Fee et al. 1985). The epiphyton algae (*Tabellaria flocculosa, Achnanthes minutissima*) and epipelon algae (consisting largely of *Nitzschia dissipata* and *Oscillatoria*) show spring and fall peaks in densities (Moore 1980). Zooplnkton are dominated by Copepoda (*Diaptomus sicilis, Diaptomus ashlandi*), Cyclopoda (*Bicuspidatus thomasi*) and Cladocera (*Daphnia longiremis*) (Muir et al. 2009, unpublished data). *Mysis relicta* is also an important crustacean Important benthic fauna of GSL include Amphipods (*Pontoporeia affinis, Gammarus limnaeus*), Chironomidae (*Chironomus*), Gastropoda (*Valvata sincera, Gyraulus parvus*), Oligochaeta (*Tubifex*) and Sphaeriidae (*Pisidium conventus, Pisidium subtruncatum*) (Larkin 1948, Rawson 1953, Muir et al. 2009, unpublished data). There are at least 25 fish species in the lake (Keleher 1972), however, some species only occur in the main lake basin. Five fish species are of commercial importance. The major commercial species are lake whitefish, (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*), inconnu (*Stenodus leucichthys*), Northern pike (*Esox lucius*) and walleye (*Sander vitreus*). Lake cisco (*Coregonus artedii*), burbot (*Lota lota*) and longnose sucker (*Catostomus catostomus*) are other important species. The highest sustained catches are from lake whitefish followed by inconnu. The eastern arm of GSL supports a trophy fishery for lake trout.

1.2- FISHERIES MANAGEMENT

GSL is a shared resource between multiple aboriginal land claim settlement areas and other harvesters. Fisheries in GSL are of many types including commercial fisheries, subsistence or aboriginal fisheries, sports fisheries, domestic fisheries and exploratory fisheries. Fisheries management in Great Slave Lake is focused on a sustainable and balanced commercial, subsistence, and sport fisheries. However, considering the size of commercial fisheries, the other types of fisheries are almost negligible. The commercial fishery on GSL has been in existence since the 1940's. Commercial fishing is allowed in the main west basin, excluding certain inshore areas (Figure 1). Area VI in the East Arm has been closed to commercial fishing since 1974 because it affected the lake trout population (Yaremchuk 1986). The commercial gillnet fishery in the West Basin is mainly for lake whitefish and the commercial fish harvest has declined since 1990 due to

a reduction in effort (Read and Taptuna 2003). This decline is not related to stock collapse or climate change but due to a decrease in effort related to production costs and low fish marketing price. However, there is a serious concern for the Buffalo River stock of inconnu, which is considered to be in the Critical Zone of the DFO Precautionary Approach framework (Day et al. 2013). The East Arm is popular as a lake trout sports fishery.

The fisheries in GSL are co-managed by the community and government departments through the Great Slave Lake Advisory Committee (GSLAC), with voting members from various resource user groups who make recommendations on allocations. The First Nations want a restructured, improved consultation process, and enhanced involvement of First Nations in management of fish stocks and the fisheries. The communities want a total review of the commercial fisheries management and want a share in the new fisheries not restricted to subsistence fisheries. Communities also want fisheries to be reviewed and managed in a harmonious manner not only taking into account the sustainable yield for whitefish but also keeping in view other species such as lake trout and inconnu.

2- CLIMATE CHANGE IMPACTS ON GREAT SLAVE LAKE

Blenckner (2005) developed a general framework and conceptual model to group and structure climatic responses of lake ecosystems. This framework consists of two main components: a landscape filter comprising the features of geographical location, catchment area and lake morphology; and an internal lake filter, comprising the features of lake history and biotic/abiotic interactions. In the GSL ecosystem, landscape filtering plays a major role. Many of the regulation-related effects on the GSL water levels, including changes in the timing and magnitude of peak levels, have been affected by climate variability. Climatic and water regulation impacts have generally counter-balanced changes in amplitude of water level fluctuations and magnitude of peak levels, but have cumulatively contributed towards earlier peak water levels in the lake (Gibson et al. 2006). The Slave River Delta in GSL is dependent on spring floods and ice jams to rejuvenate lakes and river channels, which are spawning habitat for fishes. Continued reductions in snow packs and headwater runoff are likely to reduce the frequency of flooding in the Slave River Delta (Brock et al. 2010) and will impact fish spawning.

Trends for the 20 year historical satellite records of lake ice phenology events in the Northern Canadian Lakes, including GSL show an average earlier break-up of 0.99 days per year and later freeze-up averaging 0.76 days per year (Latifovic and Pouliot 2007). The longer ice-free period may result in warmer waters and these warmer conditions could force cold-adapted specialists such as lake trout into more restricted habitats (Power et al. 2008, Vincent et al. 2011). Cold-water habitat for lake trout and lake whitefish may be shifted deeper particularly during the warmer summer months (Regier and Meisner 1990). Climate change could also result in a 50% increase in optimal growing season for lake trout in the deep east arm of GSL (McLain et al. 1994). Also, climate related changes might stress lake trout population in the relatively shallow west basin of GSL. Lake whitefish will likely be positively impacted in terms of increased growth, at least in the short term.

Increasing water temperatures within the fish thermal optimium can directly affect the physiology of freshwater fish by increasing metabolic rates and subsequently increased food consumption. Increase in metabolic activity and as a result food consumption by the fish must also increase. Therefore, any change in the growth rates of fish, especially those at upper trophic levels or keystone species, can affect not only their population but it may also result in cascading effects through the entire food web and ecosystem functions (Carpenter et al. 1985). A simulation of 3 °C increase in temperature could result in 8-fold higher food consumption for lake trout (McDonald et al. 1996). In oligotrophic lakes with minimum food availability, it may result in its extirpation. Because of warming temperatures, southerly species from the Peace and Athabasca river systems may also colonize or increase in abundance in the GSL via Slave River, which may result in a structural shift of the ecosystem.

Under climate change scenarios, Great Slave Lake can increase its seasonal evaporation by 28% (Blanken et al. 2008). A general decline in precipitation and an increase in air temperature, evaporation, and annual solar radiation in the Mackenzie River Basin will result in decreased flows and longer water renewal times for the basin lakes. With warmer water temperatures, the thermocline in lakes is expected to become more pronounced, the duration of stratification is predicted to increase and the timing, extent and duration of winter mixing are expected to decrease (Lehman et al. 2000). With climatic warming, dissolved oxygen may also be a limiting factor to fish productivity and significantly limit the availability of suitable habitat for some cold-water fishes, including lake trout (Lynch et al. 2010). Climate change and the resultant change in hydrology can also influence the Mackenzie basin chemical exports to the lakes, thus influencing in-lake processes, lake chemistry, biological components, and primary productivity (Environment Canada 2004). A shorter ice-cover period on lakes may increase the nutrient availability in summer; probably due to enhanced bacterial activity at higher water temperatures and an extended mineralization period (Blenckner et al. 2002). Shorter duration of snow and ice cover in Arctic lakes may also result in more light availability for photosynthesis and higher primary production. Increased wind-induced mixing, and increased nutrient inputs in a warmer climate may also lead to increased productivity (Hodgson and Smol 2008).

3- MODELLING FRAMEWORK

Ecopath with Ecosim (EwE) version 6.2 was used to build a model of the GSL ecosystem. Ecopath with Ecosim is a free modelling framework software program (Christensen et al. 2008) representing the complete biological ecosystem and used extensively for modeling aquatic ecosystems. It is built on assumptions of mass balance and a system of linear equations describing the average flows of mass and energy between functional groups. The software consists of mainly two main modules: Ecopath and Ecosim. Ecopath is used to construct a mass-balanced description of the food over an arbitrary period. The "mass balance" term means that the model parameters are under the physical constraint that the total flow of mass into a functional group must equal the total flow out of that group. Ecopath is effective for analyzing food web structures and trophic interactions and has been combined with other routines for trophic network analysis. The

Ecosim routine of the model is the time-dynamic module and it is used to simulate time-dynamics of trophic networks in response to management scenarios.

The basic parameterization of an Ecopath model is based on two 'master' equations representing the energy flow between functional groups and the energy balance within functional the groups.

The first master equation describes the production term for each group:

Production = catch + predation + net migration + biomass accumulation + other mortality

$P_i = Y_i + B_i \times M2_i + E_i + BA_i + P_i (1 - EE_i)$

where Pi is the total production rate of (i), Yi is the total fishery catch rate of (i), M2i is the total predation rate for group (i), Bi the biomass of the group, Ei the net migration rate (emigration – immigration), BAi is the biomass accumulation rate for (i), while M0i = Pi · (1-EEi) is the 'other mortality' rate for (i).

The second master equation is based on the principle of conservation of matter and represents the energy balance within a functional group:

Consumption = production + respiration + unassimilated food

This equation follows the productivity theory developed by Winberg (1956) according to which $Q_i = P_i + R_i + U_i$

Where Ri and Ui are the respiration and the proportion of food that is not assimilated. Using network analysis in EwE, the ecosystem network can be mapped into a linear food chain, and energy transfer efficiency can be predicted for various tropic levels. Ecopath also incorporates a number of outputs and holistic indicators for characterizing ecosystem properties and acts as indicators of ecosystem state and maturity development, and health, according to Odum's theory of ecosystem development (Odum 1969). Such indicators can be used to evaluate not only the impact of human activities, but also climate change on the ecosystem by studying the resulting changes in development and state of maturity of an ecosystem as well as to develop management policies for the future. Dynamic routines within the Ecopath (e.g. Ecosim, Ecospace and Ecotracer) rely on quantified food web structures of the ecosystem and allow explorations of the direct and indirect effects of climate change, fisheries, pollution and other anthropogenic activities on the system's biological community and its various components. More details on Ecopath can be found in Christensen et al. (2005, 2008) and and at www.ecopath.org.

4- MODEL PARAMETERIZATION

At least three of four basic parameters are required for Ecopath model: biomass estimates (B), biomass turnover rates or production/biomass ratios (P/B), consumption/biomass ratios (Q/B) and ecological efficiencies (EE). These are required for the model parameterization for each group. If one of those parameters is unknown, the Ecopath can provide its estimates using mass balance routine. Another important data input which represents the trophic interactions, is the diet composition. Dietary metrics are required for all the consumer functional groups. For each predator, the relative

proportion of the diet for each type of prey is entered in the matrix. Catch data are required for harvested species. Harvest of functional groups is also entered as landings and discards for different fleets. When appropriate, the users need to provide estimates of biomass accumulation (default is zero). This preliminary model was constructed using the published and unpublished data in technical reports, scientific publications and unpublished data mostly from 80's and 90's. Therefore, it gives a snapshot of roughly what the GSL ecosystem looked like during the last decades of 20th century (approximately 1985-1995). The model also can be run time-dynamically using Ecosim and tuned to new data to estimate changes over 20 years' time going forward.

4.1- FUNCTIONAL GROUPS

A functional group in Ecopath model can be a species, life stage of a species or group of ecologically related species. Nineteen functional groups were initially used to represent the GSL ecosystem model. These included one primary producer group, two zooplankton groups, two benthic invertebrate groups, and thirteen fish groups. Detritus, as a nonliving group, was also included. Keleher (1972) documented 24 fish species that utilize habitats within GSL, at least during a portion of their life history. For the purpose of this report. we only used the fish species, as functional groups, that remain in the lake basin during most of their life cycle and which have an important role in the fisheries and trophic ecology of the lake ecosystem. The important fish functional groups included lake trout, lake whitefish, lake cisco, longnose sucker, Northern pike, Arctic grayling, round whitefish, burbot, walleye, inconnu, lake chub (*Couesius plumbeus*) and sculpins (*Cottus cognatus* and *Myoxocephalus quadricornis*). Other important forage fish species, including ninespine stickleback (*Pungitius pungitius*), spottail Shiner (*Notropis hudsonius*) and other minnows, were combined together as other fish. Existence of morphotypes of lake trout (Zimmerman et al. 2006) and cisco (Muir et al. 2009, 2013) in GSL has been established but no detailed documented data are available on ecological differences or abundance of these two forms. Therefore, for this preliminary model these species were not divided into different morphs. Fish functional groups were not divided into multi-stanza groups because of data constraints. Invertebrates were divided into four functional groups, including mysids (*Mysis relicta)*, amphipods (*Gammarus lacustris* and *Pontoporeia affinis*), other benthos (gastropods, insect larvae, chironomids, midges, - bivalves?, and oligochaetes) and zooplankton. Important groups at 1st trophic level were primary producers and detritus. The details of 19 functional groups used to represent GSL ecosystems are in Table 1.

4.2- PRIMARY PRODUCTION

Estimates from Fee et al. (1985) were used to calculate primary production and phytoplankton biomass in GSL. Vadeboncoeur et al. (2008) demonstrated that benthic primary production might not be a substantial or negligible component of whole lake primary production in deep oligotrophic lakes. Macrophytes make a very low contribution to higher trophic levels. Therefore, in the absence of substantial quantitative data on macrophytes and periphytons, we considered only the phytoplankton as a source of primary production in the GSL ecosystem.

4.3- FISH

Fish population dynamics, including growth parameters were mostly derived from local data available from a variety of sources (Bond 1974, Falk et al. 1980, Gillman and Roberge 1982, Babaluk et al. 1983, Roberge et al. 1985, Day and Low 1993, Stewart et al. 1999, Richardson et al. 2001, Golder Associates Ltd. 2010, 2011).

Production/biomass ratio (P/B) is difficult to estimate directly. For the populations under equilibrium conditions the production to biomass ratio (P/B) is considered to equal the average total mortality Z (Allen 1971). For exploited fish species, linear catch curve methods were used to calculate total mortality. For unexploited fish groups, natural mortality (M) was estimated using Pauly's empirical relationship (Pauly, 1980) and was considered equal to total mortality (Z). For fish groups Consumption/Biomass (Q/B) ratios were estimated for each species using the empirical relationship of Palomares and Pauly (1989, 1998) in the Fishbase interphase (Fröese and Pauly, 2006) and fish population dynamics data derived from the above-mentioned sources. Mean annual temperature was measured using Rouse et al.'s (2003) data following the method described by Shuter et al. (1983). No actual data were available on the biomass (B) of fish functional groups in GSL. Downing at al.'s (1990) approach was used to estimate the possible biological production and standing stock biomass of the entire lake fish community. The biomass of top predators and commercial fishes were adjusted by indirect methods, keeping in view relative biomass of important fish species in experimental catches (Roberge et al. 1985) and a mass balance approach. For remaining forage fish groups, the Ecopath model estimated potential biomass assuming an ecotrophic efficiency (EE) of 0.90 for the fish groups. Fish dietary matrix (Table 3) was estimated using published literature including Vander Zanden and Rasmussen (1996), Zimmerman et al.(2009), Hartman (1992), Little et al. (1998), Scott and Crossman (1973), Stewart et al. (2007 a,b) and Fishbase (www. fishbase.org; Fröese and Pauly, 2006). To get the model balanced, the diets of predators were adjusted a little because information on diets from the literature for many groups was mostly qualitative. Therefore, with this inherent uncertainty it provided the opportunity to make adjustments.

4.4- INVERTEBRATE FAUNA

Gammarus lacustris and *Pontoporeia affinis*, which form almost 60% of the total benthic fauna were grouped as a separate functional group as amphipods. There is a lack of data on abundance or biomass of the whole lake benthic fauna. All other benthic fauna including *Gastropoda*, *Oligochaeta* and *Chironomidae* were grouped together as other benthos. Muir et al. (2009) analysed the macro-invertebrate data in some parts of GSL. The mean values of their analysis were assumed to represent whole GSL and were used to calculate biomass. P/B ratios were calculated after the empirical relationship of Brey (1999, 2001) for lake benthic invertebrates. Diets of amphipods and mysids were estimated after Moore (1977) and Kitchell et al. (2000). Diets of other groups were taken from the literature including Moore (1979) and Kitchell et al. (2000). Rawson (1956) studied the net plankton of GSL, including phytoplankton and zooplankton. No comprehensive study has been conducted on GSL to estimate zooplankton abundance or biomass. In the absence of substantial data, assuming EE as 0.90 (Christensen et al. 2005), the Ecopath model calculated the minimum possible biomass of mysis and zooplankton. Mean P/B ratio for zooplankton were taken from the literature with the similar environments (Waters 1977, Jorgensen 1979, Kitchell et al. 2000).

4.5- DETRITUS

Detritus includes dead matter (discards, dissolved and particulate organic matter) that are eaten by the living groups in the model. In absence of any data on detritus or on the microbial loop in the GSL ecosystem, the detrital biomass was calculated as a function of primary production and euphotic depth by employing the following relationship by Christensen and Pauly (1993):

$$\text{Log } D = 0.954 \text{logPP} + 0.863 \text{logE} - 2.41$$

Where D= detrital biomass ($g.m^{-2}$); PP = primary production (in g C m^{-2} y^{-1}); E = euphotic depth in meters.

4.6- HARVEST DATA

Mean commercial landings data for harvested species were extracted from Read and Taptuna (2001) for the period of 1990-2000. Discards from commercial fisheries were estimated as described by Deninu K'ue Development Corporation (DKDC 1994) while discards for long-nose sucker, cisco and burbot were estimated from traditional fisheries knowledge survey information (M. Y. Janjua 2011-2012, personal communication). Subsistence fisheries are not monitored regularly and harvest statistics are not available. Traditional knowledge surveys and recent evidence suggests that the subsistence harvest was less than 5% of the total for the commercial harvest (Tallman and Friesen 2007) for the modelling period with whitefish making up 68% of the overall subsistence catch.

4.7- BALANCING THE MODEL

In Ecopath, the degree of energy 'imbalance' of each functional group is usually determined by examining the ecotrophic efficiency (EE). A value of EE greater than 1 indicates that total demand exceeds total production and hence the model is in imbalance. To adjust imbalance, adjustments to the diet were made first and if required, then changes to B, P/B or Q/B were made. It was ensured that all the model parameters complied with physiological and thermodynamic constraints using two other important diagnostic indices including Gross food conversion efficiency (P/Q) ranging from 0.1 to 0.3 and Production/Respiration (P/R) ratio ranging from 0 to 1.

4.8- MODEL VALUATION

Pedigree analysis in EwE was used to address and quantify uncertainties of input parameters. The key criteria used were based on the assumption that the input parameters estimated from local data are better than the data from elsewhere or derived from empirical relationships. These criteria were checked for biomass, P/B, Q/B ratio, diet composition and catches (Figure 2). The present Ecopath model has a pedigree index of 0.41, which seems to be in the upper range (0.16-0.68) of 150 Ecopath model studies by Morissette (2005, 2007). It indicates that the model is made on inputs derived from both local and literature-based information from other ecosystems.

5- TROPHIC NETWORK ANALYSIS

The basic input and output parameters for all the groups in the model are shown in Table 2. Thermodynamic constraints limit the realized range of production/respiration (P/R), respiration to assimilation (R/A) and respiration/biomass (R/B). These metrics must be lower than 1. In our model these ratios satisfied the requirement of a balanced ecosystem model and was used as one of the criteria to accept the present Ecopath solution. The trophic levels (TLs) assigned by the model to the functional groups vary between 1.0 and 4.1 (Figure 3). Predators at the higher trophic level, lake trout and inconnu, were followed by pike, walleye and burbot. Almost all the fish groups were at trophic level above TL 2.9. Invertebrate groups including mysids, zooplankton, amphipods and other benthos were classified to TLs between 2.0 to 2.5.

5.1- FLOWS AND BIOMASS

Overall, average fish biomass density obtained from the GSL ecosystem model is 1.86 t km^{-2}. In terms of biomass, lake whitefish, followed by cisco and sucker, dominate the ecosystem. Ecopath models estimated potential biomass of lake cisco and deep-water sculpin by assessing the demands of predators and the amount of fish which can be supported by lower trophic levels and was estimated as 14% and 12%, of the total fish biomass respectively. These results might look a bit overestimated if we compare this with experimental catches in these lakes. However Rawson (1951) and Roberge et al. (1985) found lake cisco to be one of the fish species dominant in abundance and biomass. Sculpin is difficult to catch in GSL, but various observations suggest that it is present in large numbers near the bottom in the deep water (Rawson 1951). In GSL, EE of lake cisco and sucker calculated by Ecopath models was very high. It revealed that they were constrained by predation or their biomass was estimated at a minimum level. At lower trophic levels, amphipods and mysids biomass were dominant. Wide ranges (0.05-0.27) of P/Q or gross food conversion efficiency ratios are found in the system with a high ratio for lake whitefish. The Ecopath model aggregates the system into discrete trophic levels, and trophic flows and it shows that phytoplankton and detritus were both important for the functioning of the ecosystem with 58% flows at TL I that originate from phytoplankton while 42% originate from detritus (Table 4). Zooplankton dominate the energy flows at TL II followed by other benthic fauna and amphipods, while flows from mysids were dominant at trophic level III. Recycling is an important positive mechanism in mature ecosystems (Vasconcellos et al. 1997). Trophic network analysis indicates that recycled throughput occurred at TL I and TL II and this gives support to the stability of the lake ecosystem. A total of 36.27 t km^{-2} y^{-1} of detritus was consumed by TL II and 29.46 t km^{-2} y^{-1} was returned to the detritus, indicating that TL II plays a significant role in system recycling. The maximum flows to detritus were from phytoplankton followed by zooplankton and mysis. Throughput passes TL I and TL II accounted for 96.93% of total system throughput. It shows the existence of a loop in the detritus and the TL II. The loop explicitly increased the recycling of the system thereafter, which increased the stability of the system.

The 'Lindeman spine' analyses developed by Ulanowicz (1995) reduces the complex food webs into a simple chain of trophic interactions and also can be used to calculate transfer efficiencies between trophic levels (Figure 4). The geometric means of the transfer efficiencies of the flows originating from detritus and the primary producers

through the trophic levels II-IV, are approximately 8.9% and 8.5%, respectively with a mean value of 8.8% which is close to the universal 10% value (Table 5).

5.2- ECOSYSTEM INDICES AND ATTRIBUTES

The Ecopath results can be used to evaluate the whole ecosystem state in terms of its productivity, complexity, efficiency, and health. Several indices of ecosystem maturity, stability and resilience indices can be been derived from EwE mass-balanced models (Christensen 1995) and these system indices can be used to study the impact of fisheries and climate change at the ecosystem level. Key ecosystem attributes derived from the GSL Ecopath model are presented in Table 6. Total respiration is an index of a system's activity and it is usually high in perturbed ecosystems and low in mature and stable ecosystems (Christensen et al. 2005). In the GSL ecosystem, the sum of all respiratory flows was 82 $t.km^{-2}.y^{-1}$ which is higher than pristine Great Bear Lake (GBL) (28.3 $t.km^{-2}.y^{-1}$, unpublished work), but much lower than Lake Superior (610 $t.km^{-2}.y^{-1}$, Kitchell et al. 2000 model), or Lake Ontario (988 $t.km^{-2}.y^{-1}$, Halfon and Schito 1993). The total net primary production was estimated to be 253 $t.km^{-2}.year^{-1}$, almost five times higher than Great Bear Lake and six times less than Lake Superior, two comparative ecosystems. Total throughput is the sum of all imports and exports, consumption and flows in an ecosystem and is a measure of ecosystem size (Ulanowicz 1986). For GSL the total throughput was 601 $t.km^{-2}.year^{-1}$, which is five times higher than GBL and six times lower than Lake Superior. With development and maturity, ecosystems develop from linear to complex food webs (Odum 1969). The connectance index (CI), which is a measure of the percentage of realized links over the number of possible links, and the system omnivory index (SOI), which shows how feeding interactions are distributed between trophic levels can be used as indicators of food web complexity (Christensen and Pauly 1998). Connectance Index for GSL (0.25) was higher than Lake Superior and Lake Ontario. The System omnivory index for GSL (0.08) indicates a more likely linear food chain structure. Gross efficiency of fisheries (catch/PP) is higher in systems fished low in the food web (lower trophic levels) and low in systems fished higher in trophic levels (Christensen et al. 2005). The gross efficiency of fisheries in GSL was higher than other Great Lakes in Canada because more than 80% of the catches were composed of lake whitefish and the trophic level of catch (TLc) was lower (3.24) as compared to Great Bear Lake (3.56), Lake Superior (3.52), and Lake Ontario (3.82).

Primary production/respiration (Pp/R) and primary production/biomass (Pp/B) are related to ecosystem maturity as energetic attributes. In the early stages of ecosystem development, primary production (Pp) is more than respiration (R), therefore (Pp/R) ratio will be greater than 1. However, with maturity this ratio decreases until respiration and and primary production are equivalent. The total primary production to total respiration ratio for the GSL ecosystem was greater than one (3.24) which indicates that system production exceeds respiration. The conclusion that GSL is not a mature system on Pp/R basis is uncertain because we excluded bacterial activity and this might increase respiration and thus balance the equation (Christensen and Pauly 1993). With system maturity, biomass also accumulates and as a result, the biomass/primary production (B/Pp) ratio increases. The relatively higher value of B/Pp (0.060) in the GSL ecosystem indicates accumulation of biomass over time and system stability. However, this value is much less than comparatively pristine GBL ecosystem (0.20, unpublished work) The

biomass/total throughput ration (B/T) for GSL (0.026) is lower than GBL (0.07) but much higher than Lake Superior (0.004) and Lake Ontario (0.003), showing that comparatively much less energy flow is required to support the biomass in the GSL ecosystem.

The degree of recycling in an ecosystem can be measured with Finn's Cycling Index (FCI), which expresses the fraction of the total system throughput that is recycled (Finn 1976, Christensen and Pauly 1993). Christensen (1995) found a strong correlation between the FCI and the ecosystem maturity rankings. The FCI value for the GSL ecosystem (3.33) is higher than Lake Superior (0.39, Kitchell et al. 2000) model and Lake Ontario (2.630, Halfon and Schito 1993) showing its comparative stability. Ascendancy accounts for both size and organization of the system and is a measure of ecosystem efficiency. Ascendency is higher in mature and complex systems (Vasconcellos et al. 1997). The total ascendency of the GSL ecosystem primarily consists of the internal flows (41% of the total fluxes), followed by the export (35%), and the respiration (23%) (Table 7). The relative ascendancy (ascendency/capacity) for GSL (0.38) was lower than Lake Superior (0.50) and Lake Ontario(0.49), an indication of its ecosystem maturity and stability. The internal redundancy (the overhead on internal flow, 46%) and the system overhead (62% of the development capacity) are high and it indicates that GSL possesses significant reserves to overcome substantial external disturbances.

5.3- MIXED TROPHIC IMPACT AND KEYSTONENESS

The mixed trophic impacts (MTI) are indicators of the relative impact of change in the biomass of one functional group on the other functional groups of the ecosystem. MTI are calculated by multiplication of the matrix of the direct impacts compiled by using the matrices of positive direct impact of diet and negative direct impact of consumption (Ulanowicz and Puccia 1990). The indirect impacts can also be associated with inter-group competitions and trophic cascades. The mixed impact is a sum of these direct and indirect impacts. Trophic network analysis shows that pike, burbot and benthic fauna have key roles in the GSL ecosystem. Top predators, especially pike and burbot, have a negative impact on almost all fish functional groups while cisco and the other forage fish group have positive impacts on top predators. Benthic fauna also have a strong positive impact on fish groups at middle trophic levels. Because of their relatively low abundance, some fish groups such as Arctic grayling, round whitefish and lake chub have almost no impact on the rest of the food web. Detritus and phytoplankton appear to have a positive impact on the invertebrate functional groups, which is transmitted throughout the food web. MTI can be used as indicator of direct and indirect effects of fishing. Commercial fishing negatively influenced most predatory fish groups; however, the fisheries impact was positive on forage fish groups at mid trophic levels because of elimination of their predators.

Keystone species are defined as relatively low biomass species with a structuring role in their food webs. Libralato et al. (2006) introduced the keystoneness (KS) index which scales the impact of a group on the whole ecosystem through attributing high values to stocks having large impacts while maintaining a comparatively low biomass. In GSL, burbot and pike were found to be the main keystone species, having relative higher impact and therefore could have an important role in maintaining the structure of its

ecosystem (Figure 6). Keystone species are very important from a climate change prospective because a strong response to climate by keystone species may have dramatic effects on the food web structure especially in simple linear food chains (Blenckner 2005). Lake trout act as a keystone predator in many Arctic lakes (McDonald et al. 1996). However, in GSL, the keystoneness index of lake trout was very low compared to other predators. However, historically GSL supported profitable lake trout fisheries. Even though they are not the top keystone species, their importance commercially and as a potential ecosystem engineer necessitates evaluation of lake trout on the structure of the GSL ecosystem. Burbot are known to have an important role in regulating lake ecosystems (Carl and McGuiness 2006, Jacobs et al. 2010, Cott et al. 2011) and have functioned in a keystone role in other great lakes including Lake Ontario (Brandt 1986) and Lake Michigan (Madenjian et al. 2005).

5.4- PRIMARY PRODUCTION REQUIRED (PPR)

Primary production required (PPR) is the energy required to support consumption or catches in the ecosystem and is an index of the ecosystem efficiency similar to the "emergy" concept (Pauly and Christensen, 1995). Estimates of primary production (PPR) required to sustain fisheries are based on trophic level of catch, TLc, energy transfer efficiency between trophic levels, and the primary productivity. Primary production required to sustain fisheries has been conceived as an ecological foot print. Percent PPR (PPR as a part of Total PP) in combination with TLc is a quantitative ecosystem index to capture the effect of fisheries (Pauly and Christensen 1995, Tudela et al. 2005). The sensitivity of an ecosystem to fisheries depends on both TLc and % PPR. The present study showed that the GSL fisheries require 3.13 % of the total primary production, which is a small proportion of the productive capacity of the ecosystem. Moderate TLc and low % PPR indicates that the fishery during the modeling period was in a sustainable range. In the GSL ecosystem, maximum primary production per unit catch was required for the harvest of walleye and lake trout while the minimum was required for lake whitefish (Table 8). Much lower per unit cost for GSL whitefish shows why its fishery is ecologically less expensive and hence much stable and sustainable.

6- MODEL SIMULATIONS

6.1- PRELIMINARY FISHERIES SIMULATIONS

We observed the GSL Ecosim model working under different fishing scenarios. At present, the fishing in GSL is reduced to almost 25% of the modeled time period because of socioeconomic constraints (Freshwater Fish Marketing Corporation unpublished data). We simulated this fishing scenario over a 20-year period by reducing the overall fishing effort to 25% and observed the changes in relative biomass trajectories of fish functional groups. In absence of any time series data to adjust vulnerabilities, the simulations were ran with two sets of Ecosim's vulnerabilities to predation; firstly, where with all vulnerabilities were set to 2.0 (Ecosim default) and secondly where all vulnerabilities were adjusted as 3 to imply stronger predator-prey interactions. With default vulnerabilities, lake trout showed 50% and inconnu showed 28% initial increase in relative biomass (Figure 7). This is because in the model, fishing mortality accounts for a large proportion of the total mortality of these groups. Lake whitefish also showed a 10% increase. Lake cisco showed a 15% reduction, with decreased fishing. By adjusting

vulnerabilities to 3, to imply stronger predator-prey interactions, there was a substantial increase in relative biomass of lake whitefish (almost 50%). During a recent traditional fisheries and environment knowledge survey conducted by the authors (TEK, Unpublished), communities along the GSL observed an increase in the lake trout and inconnu populations, while some decrease in the cisco population was predicted by the model. When comparing results of these initial simulations with fresh knowledge, it appears that this initial model is quite stable and will serve as a background for further development of better more realistic models to inform decision makers.

6.2- CLIMATE CHANGE SIMULATIONS

Climate change can have impacts at different levels of the food web that include changes in plankton production, in the spatial distributions of organisms, in recruitment success of functional groups or changes in the biodiversity and ecological niches. Primary production is critical in maintaining ecosystem diversity and supporting fishery resources and can cause predictable changes in the biomass of groups in the ecosystem. Bottom-up trophic flow control tends to be dominant in aquatic ecosystems (Cury et al. 2003). However, it is difficult to predict the magnitude and direction of response of different groups to changes in primary production because of trophic interactions including predation and computation. In Arctic and sub-Arctic lakes, primary productivity will probably increase because it is correlated with high temperatures, nutrient loadings, as well as a longer ice-free season and more sunlight (Wrona et al. 2006). However, there is a general uncertainty about the expected environmental changes in the GSL area under a range of possible future climate change scenarios. In the absence of any regional data or model, it is difficult to predict changes in mean annual primary production rate. Therefore, we focussed our preliminary simulations on an increase or decrease in primary productivity rate as a first-order impact and the subsequent impacts on the other functional groups. We did preliminary simulations using the Ecosim linear forcing function on the rate of primary production to specify a temporal increase and decrease in the percent primary production over 50-year periods. A range of change from -15% to +15% in primary productivity was simulated from the model's static values. Preliminary simulations indicate an overall linear response of functional groups to change in primary productivity (Figure 8). There was a change in the relative biomass of functional groups under the increased and decreased primary productivity induced scenario; however, the scale of the increases was not the same for all groups. The largest change was observed in the whitefish biomass and minimum change was recorded walleye and lake trout. However, the role of predation and competitive interactions may be underestimated in such types of simulations when data are not available for time series fitting and adjustment of vulnerabilities. Therefore, it is important and necessary to acquire adequate time-series data to parameterize predation and competition interactions that would be helpful to estimate and adjust vulnerability parameters using real trends.

7- FUTURE WORK AND CONCLUSION

The common ecosystem modelling approach is to start building a model on available data, information, and scientific expertise. These initial models serve as a background for further development of a better and more realistic model. This preliminary model is an important contribution to integrate the available data and provide a base on which new data can be introduced to improve the model results. There are some

knowledge gaps and data limitations both at the lower and upper trophic levels and as a result, many uncertainties are associated with this preliminary model for the GSL ecosystem. As is typically the case for whole ecosystem models most of the input parameters used have very wide ranges of variation. Even in a data rich situation, there can be high uncertainty related to the inputs, and it results in uncertainty to outputs of the models (Morissette 2005). Essington (2007) divided EwE studies into two main categories, the first one is heuristic use, where the model can be used to elucidate trophic interactions and to highlight the implications of management on these interactions and the second one is a predictive approach which is used to explore fisheries policy responses on the fish community. According to Essington (2007), the latter use raises more issues of model credibility, and associated uncertainties with simulations and predictions as compared to heuristic use.

Keeping in view the uncertainties associated with a preliminary model, our present analyses are focused more on the characterization of the basic ecosystem attributes and flows in the GSL ecosystem. This approach has heuristic value as it provides knowledge of how ecosystem resources interact. This information is important to highlight the ecosystem structure and functions. The results of this initial model look quite realistic and can be used by management as a heuristic approach such as to study basic interactions in the food web, ecosystem attributes and sustainability. The Ecopath model is a dynamic tool and its modelling framework will allow future users to change model assumptions based on the available data, including climate change predictions, and review the possible impacts on fisheries and the ecosystem. Our model provides a base that can be upgraded as new information becomes available. As well, we are well on the way towards the development of a reliable ecosystem model that will be able to contribute to management strategy evaluations. Research on the diversity, productivity, growth, and biomass of different functional groups in the GSL ecosystem under the NWT-Cumulative Impact Monitoring Program (CIMP) project and DFO annual monitoring is ongoing. Results from these projects in coming years will be helpful in improving of this model by the addition of new input data that will test our results. GSL is divided into different management areas based on stocks and habitats. To further facilitate fisheries management, data based on management areas and grids will be helpful in dividing this whole lake model into sub-models for each management area and will make possible the use of the Ecospace module. The Ecospace extension of the Ecopath model allows a compartmentalization of biomass across a 2D-grid according to habitat preferences. It then can be used to study the spatial impact of climate change especially when warmer conditions could force cold-adapted specialists such as lake trout into more restricted habitats in deep waters.

There is also a lack of time-series data particularly related to biomass and primary productivity. Such data are very important for adjustment and improvement of the Ecosim model. The Ecosim model fitted to time series provides a better base for simulation and is useful to provide outputs that are more realistic, especially in changing climate scenarios. Time series fitting can be used to estimate the vulnerability of each prey species to its predators. The process improves the goodness of fit between model predictions and observed time series data for the different ecosystem components in contrasting situations by adjusting the vulnerability parameters. Therefore, an Ecosim

model fitted to time series obtains a more realistic vulnerability matrix. There is lack of a proper primary production time series or any regional model that can predict change in aquatic primary production in lakes. However, the color of the water body can be related to the concentration of chlorophyll *a* and by knowing the chlorophyll *a* concentration of a body of water we can predict its primary productivity. Therefore, use of remote sensing data from the past and present has the potential to address this data gap in a cost effective manner.

The framework for the assessment of climate change impact on an ecosystem is made up of three steps: assessment, forecast, and management. Starting with the assessment component we have identified important functional groups and constructed a preliminary ecosystem structure model. With the availability of new data from ongoing monitoring, this model will be further improved in coming years: outputs from the Ecopath model and Ecosim scenarios will forecast future ecosystem structure that can be used for risk analysis for adaptive management.

8-REFERENCES

Allen, K.R. 1971. Relation between production and biomass. J. Fish. Board Can. 28: 1573-81.

Babaluk, J.A., Craig, J.F. and Campbell, J.S. 1993. Age and growth of estimation of walleye, *Stizostedion vitreum* using opercula. Manuscr. Rep. Fish Aquat. Sci. 2183. 31 p.

Blanken, P.D., Rouse, W.R. and Schertzer, W.M. 2008. The time scales of evaporation from Great Slave Lake. *In* Cold region atmospheric and hydrologic studies. The Mackenzie GEWEX Experience, Edited by M.K. Woo. Springer-Verlag Berlin pp. 81-196.

Blenckner, T. 2005. A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia 533: 1-14.

Bond, W.A. 1974. Data on ciscoes, burbot and longnose suckers from Great Slave Lake, Northwest Territories. Can. Fish. Mar. Serv. Data Rep. Ser. CEN/D-74-3. 44 p.

Brandt, S. B. 1986. Disappearance of the deepwater sculpin (*Myoxocephalus Thompsoni*) from Lake Ontario: The keystone predator hypothesis. J. Great Lakes Res. 12: 18-24.

Brey, T. 1999. Growth performance and mortality in aquatic benthic invertebrates. Adv. Mar. Biol. 35, 153 - 223.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. Alfred Wegener Institute for Polar and Marine Research, Germany.

Brock, B.E., Martin, M.E., Mongeon, C.L., Sokal, M.A., Wesche, S.D., Armitage, D. Wolfe, B.B., Hall, R.I. and Edwards, T.W.D. 2010. Flood frequency variability during the Past 80 Years in the Slave River Delta, NWT, as determined from Multi-Proxy Paleolimnological Analysis. Can. Water Resour. J. 35: 281-300.

Carl, L.M. and McGuiness, F. 2006. Lake whitefish and lake herring population structure and niche in ten south-central Ontario lakes. Environ. Biol. Fish. 75: 315-323.

Carpenter, S. R., Kitchell, J. F. and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience 35: pp. 634-639.

Christensen, V. 1995. Ecosystem maturity-towards quantification. Ecol. Model. 77: 3-32.

Christensen, V. and Pauly, D. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecol. App. 8: 104-109.

Christensen, V. and Pauly, D. 1993. Trophic models of aquatic ecosystems . The World Fish Center. 390 p.

Christensen, V. Walters C.J. and Pauly, D. 2005. Ecopath with Ecosim: A user's guide, Fisheries Centre, University of British Columbia, Canada, 154 p.

Christensen, V. Walters, C.J., Pauly, D. and Forrest, R. 2008. Ecopath with Ecosim version 6 User Guide. Lenfest Ocean Futures Project. Fisheries Centre, University of British Columbia, Vancouver, Canada, 235 p.

Cott, P. A., Johnston, T. A. and Gunn, J. M. 2011. Food web position of burbot relative to lake trout, Northern pike, and lake whitefish in four sub-Arctic boreal lakes. J. Appl. Ichthyol. 27: 49-56.

Cury, P.M., Shannon, L.J. and Shin, Y. J. 2003. The functioning of marine ecosystems: a fisheries perspective. *In* Responsible Fisheries in the Marine Ecosystem. Edited by M. Sinclair and G. Valdimarsson FAO and CABI Publishing UK. pp. 103-123.

Day, A.C. and Low, G. 1993. The Great Slave Lake commercial inconnu, *Stenodus leucichthyes*, Fishery. AFSAC Doc. 1992/93-07, 48 p.

Day, A.C., VanGerwen-Toyne, M. and Tallman, R. F. 2013. A risk-based decision-making framework for Buffalo River Inconnu (*Stenodus leucichthys*) that incorporates the Precautionary Approach. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/070. 13 p.

Deninu K'ue Development Corporation (DKDC). 1994. The freshwater fishery. Great Slave Lake. Fisheries Arctic Development Library 3-11-46.

Downing, J. A., Plante, C. and Lalonde, S. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. 47: 1929-1936.

Essington, T.E. 2007. Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. Can. J. Fish. Aquat. Sci. 64: 628-637.

Evans, M.S. 2000. The large lake ecosystems of Northern Canada. Aquat. Ecosyst. Health. 3: 65-79.

Falk, M. R., Gillman, D.V. and Dahlke, L.W. 1973. The 1972 sports fisheries of Great Bear and Great Slave lakes, N.W.T. Environ. Can. Fish. Mar. Ser. Tech. Rep. Series. No. CEN/T- 73-8: 100 p.

Falk, M.R. and Gillman, D.V. 1975. Data on the lake and round whitefish, lake cisco, northern pike, Arctic grayling and longnose sucker from the East Arm of Great Slave Lake, NWT, 1971-74. Can. Fish. Mar. Serv. Data Rep. Ser. 75. 95 p.

Falk, M.R., Gillman, D.V. and Read C.J. 1980. The walleye, *Stizostedion vitreum* (Mitchill), sport fishery on Mosquito Creek, Northwest Territories, 1973-1978. Manuscr. Rep. Fish Aquat. Sci. 1559. 29 p.

Fee, E., Stahwon, M. P. and Kling, H. J. 1985. Primary production and related limnological data for some lakes of the Yellowknife, NWT area. Can. Tech. Rep. Fish. Aquat. Sci. 1409. 55 p.

Froese, R. and Pauly, D. (Eds.), 2009. FishBase. World Wide Web electronic publication. www.fishbase.org, version (01/2009).

Fuller, W. A. 1955. The inconnu (*Stenodus leucichthys mackenziei*) in Great Slave Lake and adjoining waters. J. Fish. Res. Board Can.12: 768-780.

Gibson, J.J., Prowse, T.D. and Peters, D.L. 2006. Partitioning impacts of climate and regulation on water level variability in Great Slave Lake. J. Hydrol. 329: 196-206.

Gillman, D. V. and Roberge, M.M. 1982. Creel census and biological data from the lake trout sport fishery on Great Bear and Great Slave Lake Northwest Territories, 1980. Can. Data Rep. Fish. Aquat.Sci. 338. 24 p.

Golder Associates Ltd. 2010. Miramar Northern Mining Ltd. Con Mine Environmental effect monitoring Phase 3: Investigation of Cause. Prepared for Miramar Northern Mining Ltd. Con Mine Ltd. Prepared by Golder Associates Ltd., Yellowknife, NT. 55 p.

Golder Associates Ltd. 2011. Giant Mine, Environmental Effects. Monitoring - Phase 3. Submitted to Environment Canada by Indian and Northern Affairs Canada, NWT Region, Report Number: 10-1328-0057. Prepared by Golder Associates Ltd., Yellowknife, NT. 101 p.

Halfon, E. and Schito, N. 1993. Lake Ontario food web, an energetic mass balance. In Trophic Models of Aquatic Ecosystems. Edited by V. Christensen and D. Pauly. ICLARM, Manila. pp. 29-32.

Hodgson, D.A. and Smol, J. P. 2008. High latitude paleolimnology. *In* Polar lakes and Rivers-Limnology of Arctic and Antarctic aquatic ecosystems. Edited by W.F. Vincent, and J. Laybourn-Parry. Oxford University Press Oxford. pp. 43-64.

Jacobs, G.R., Madenjian, C.P., Bunnell, D.B. and Holuszko, J.D. 2010. Diet of lake trout and burbot in Northern Lake Michigan during spring: evidence of ecological interaction. J. Gt. Lakes Res. 36: 312-317.

Jorgensen, S.E. 1979. Handbook of Environmental Data and Ecological Parameters. International Society of Ecological Modelling Copenhagen. 1162 p.

Keleher, J.J. 1972. Great Slave Lake: effects of exploitation on the salmonid community. J. Fish. Board Can. 29: 741-753.

Kitchell, J. F., Cox S.P., Harvey, C.J., Johnson, T.B., Mason, D.M , Schoen, K.K., Aydin, K., Bronte, C., Ebener, M. and Hansen, M. 2000. Sustainability of the Lake Superior fish community: interactions in a food web context. Ecosystems 3: 545-60.

Larkin, P. A. 1948. *Pontoporeia* and *Mysis* in Athabaska, Great Bear and Great Slave Lakes. B. Fish. Board. Can. 8: 1-33.

Latifovic, R. and Pouliot, D. 2007. Analysis of climate change impacts on lake ice phenology in Canada using the historical satellite data record. Remote Sens. Environ. 106: 492-507.

Lehman J.T., Brooks A.S. and Zastrow J.C. 2000. Water Ecology. *In* Great Lakes Regional Assessment Report. Preparing for a Changing Climate: The Potential Consequences of Climate Variability and Change in the Great Lakes Region. Edited by P. J. Sousounis and J. M. Bisanzm. University of Michigan Atmospheric, Oceanic, and Space Sciences Department. Ann Arbor, MI. pp. 43-50.

Libralato, S., Christensen, V., and Pauly, D. 2006. A method for identifying keystone species in food web models. Ecol. Model. 195: 153-171.

Little, A. S., Tonn, W. M., Tallman, R. F., and Reist, J. D. 1998. Seasonal variation in diet and trophic relationships within the fish communities of the lower Slave River, Northwest Territories, Canada. Environ. Biol. Fish. 53: 429-445.

Low, G. and Read, C. J. 1987. Data from the Commercial Fishery for Lake Whitefish, *Coregonus clupeaformis* (Mitchill), on Great Slave Lake, Northwest Territories, 1983 and 1984. Can. Data Rep. Fish. Aquat. Sci. 641

Low, G., Stewart, D.B., Day, A.C. and Taptuna, W.E.F. 1999. Comparison of fish harvests from the east arm of Great Slave Lake, N.W.T., by itinerant sport anglers in 1986 and 1994. Can. Fish. Aquat. Sci. Tech. Rep. 2263.

Lynch, A. J., Taylor, W. W. and Smith, K. D. 2010. The influence of changing climate on the ecology and management of selected Laurentian Great Lakes fisheries. J. Fish Boil. 77: 1764–1782.

Madenjian, C. P., Hondorp, D. W., Desorcie, T. J. and Holuszko, J. D. 2005. Sculpin community dynamics in Lake Michigan. J. Gt. Lakes Res. 31: 267-276.

McDonald, M. E., Hershey, A. E. and Miller, M. C. 1996. Global warming impacts on lake trout in arctic lakes. Limnol. Oceanogr., 41: 1102-l 108.

McLain, A.S., Magnuson, J.J. and Hill, D.K. 1994. Latitudinal and longitudinal differences in thermal habitat for fishes influenced by climate warming: expectations from simulations. Verh. Internat. Verein. Limnol. 25: 2080-2085.

Mohr, L.C. 1984. The general ecology of the slimy sculpin (*Cottus cognatus*) in Lake 302 of the Experimental Lakes Area, northwestern Ontario. Can. Tech. Rep. Fish. Aquat. Sci.1227: 20 p.

Moore, J. W. 1979 Influence of food availability and other factors on the composition, structure and density on a subarctic population of benthic invertebrates. Hydrobiology, 62: 215-223.

Moore, J. W. 1977. Importance of algae in the diet of subarctic populations of *Gammarus lacustris* and *Pontoporeia affinis*. Can. J. Zool. 55: 637-641.

Moore, J. W. 1980. Seasonal distribution of phytoplankon in Yellowknife. Int. Rev. Gesamten Hydrobiol. Hydrogr. 65: 283-293.

Morissette, L. 2005. Addressing Uncertainty in Marine Ecosystems Modelling. Strategic management of marine ecosystems. Edited by E. Levner, I. Linkov, J.M. Proth Springer, Netherlands. pp 127-142.

Morissette, L. 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: A comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. Thesis (Ph.D.) The University of British Columbia, Vancouver, BC.

Muir, A.M., Vecsei, P., Machtans, H.M., Gerein, K.M. and Reist, J.D. 2009. Cisco diversity in Great Slave Lake, Northwest Territories, Canada: a database and data summary (*Salmoniformes: Coregonidae*). Can. Tech. Rep. Fish. Aquat. Sci. Unpublished. 83 p.

Muir, A.M., Vecsei, P., Pratt, T.C., Krueger, C.C., Power, M. and Reist, J.D. 2013. Ontogenetic shifts in morphology and resource use of cisco *Coregonus artedi*. J. Fish Biol. 82: 600–617.

Odum, E.P. 1969. The strategy of ecosystem development. Science, 164: 262-270.

Palomares, M. L. and Pauly, D. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Aust. J. Mar. Freshw. Res. 40: 259-73.

Palomares, M. L. and Pauly, D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. J. Mar. Freshw. Res. 49: 447-453.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39: 175–92.

Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. Nature, 374: 255-257.

Power, M., Reist, J.D, and Dempson, J.B. 2008. Fish in high-latitude lakes. *In* Polar lakes and rivers, Limnology of Arctic and Antarctic aquatic ecosystems. Edited by W.F. Vincent, and J. Laybourn-Parry. Oxford University Press. Oxford.

Randall, R. G. and Minns, C. K. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Can. J. Fish. Aquat. Sci. 57: 1657-1667.

Rawson, D. S. 1950. The physical limnology of Great Slave Lake. J. Fish. Res. Board Can. 8: 3-66.

Rawson, D. S. 1951. Studies of the fish of Great Slave Lake. J. Fish. Res. Board Can. 8: 207-240.

Rawson, D. S. 1953. The bottom fauna of Great Slave Lake. J. Fish. Res. Board Can. 10: 486-520.

Rawson, D. S. 1956. The net plankton of Great Slave Lake. J. Fish. Res. Board Can. 13: 53-127.

Read, C.J. and Taptuna, W.E.F. 2001. Data from the commercial fishery for lake whitefish *Coregonus clupeaformis* (Mitchill), on Great Slave Lake, Northwest Territories, 1996/97 to 1998/99. Can. Data Rep. Fish. Aquat. Sci. 1081: 45 p.

Read, C.J. and Taptuna, W.E.F. 2003. Data from the commercial fishery for lake whitefish, *Coregonus clupeaformis* (Mitchill), on Great Slave Lake, Northwest Territories, 1999/00 to 2001/02. Can. Data Rep. Fish. Aquat. Sci. 1111: 54 p.

Regier, H. A. and Meisner, J. D. 1990. Anticipated effects of climate change on fresh-water fishes and their habitat. Fisheries 15: 10-15.

Richardson, E. S., Reist J. D. and Minns, C. K. 2001. Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on lake habitat requirements Can. Manuscr. Rpt. Fish. Aquat. Sci. 2569. 46p.

Roberge, M.M., Low, G. and Read, C. J. 1985. Data from an experimental gillnetting program on Great Slave lake, Northwest Territories, 1980-81. Can. Manuscr. Rep. Fish Aquat. Sci. 537: 156 p.

Rouse, W.R., Oswald, C.M., Binyamin, J., Blanken, P.D., Schertzer, W.M. and Spence, C. 2003. Interannual and seasonal variability of the surface energy balance and temperature of Central Great Slave Lake. J. Hydrometeor. 4:720-730.

Scott, W. B. and Crossman, E. J. 1973. Freshwater fishes of Canada. B. Fish. Res. Board Can. 184. 966 p.

Shannon, L.J., Coll, M., Neira, S., Cury, P.M., and Roux, J. P. 2009. Impacts of fishing and climate change explored using trophic models. *In* Climate Change and Small Pelagic Fish. Edited by D.M. Checkley, C. Roy, J. Alheit and Y. Oozeki. Cambridge University Press. pp. 158-190.

Sheldon, T. A. 2006. Ecology and evolution of the deepwater sculpin (*Myoxocephalus thompsonii*): conservation of a glacial relict. Thesis (M. Sc.) University of Manitoba, Winnipeg, Canada. 135 p.

Shuter, B. J., Schlesinger, D. A. and Zimmerman, A.P. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. Can. J. Fish. Aquat. Sci. 40: 1838- 1845.

Stewart, D. B., Carmichael, T. J., Sawatzky, C. D., Reist, J. D. and Mochnacz, N. J. 2007. Fish diets and food webs in the Northwest Territories: Round Whitefish. Can. Manuscr. Rep. Fish Aquat. Sci. 2794: 21 p.

Stewart, D. B., Low, G., Dewsbury, N., Read, C. J. and Day, A.C. 1999. Biological data from an experimental fishery at Resolution Bay, Great Slave Lake, Northwest Territories, June - August 1996. Can. Data Rep. Fish. Aquat. Sci. 1049: 91 p.

Stewart, D. B., Mochnacz, N. J., Reist, J. D., Carmichael, T. J. and Sawatzky, C. D. 2007. Fish diets and food webs in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). Can. Manuscr. Rep. Fish Aquat. Sci. 2796: 21 p.

Tallman, R. F. and Friesen, M. K. 2007. A review of length and age trends in lake whitefish (*Coregonus clupeaformis*) harvested from Great Slave Lake between 1972 and 1995. Can. Manuscr. Rep. Fish. Aquat. 2819: 27 p.

Tudela, S., Coll, M. and Palomera, I. 2005. Developing an operational reference framework for fisheries management on the basis of a two-dimensional index of ecosystem impact. ICES J. Mar. Sci. 62: 585-591.

Ulanowicz, R. E. and Puccia, C. J. 1990. Mixed trophic impacts in ecosystems. Coenoses, 5: 7-16.

Ulanowicz, R.E. 1986. Growth and Development: Ecosystem Phenomenology. Springer-Verlag, New York, 203 p.

Ulanowicz, R.E. 1995. Ecosystem trophic foundations: Lindeman exonerate. *In* Evolution, Order and Complexity. Edited by B.C. Patten and S.E. Jorgensen, . Routledge, London, pp. 549–560.

Vadeboncoeur, Y., Peterson, G. , Vander Zanden, M. J. and Kalff, J. 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. Ecology 89: 2542-2552.

Vander Zanden, M. J. and Rasmussen, J. B. 1996. A trophic position model of pelagic food webs: Impact on contamination bioaccumulation in lake trout. Ecol. Monogr. 66: 451-477.

Vasconcellos, M., Mackinson, S., Sloman, K. and Pauly, D. 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecol. Model. 100: 125-134.

Vincent, W. F., Callaghan, T. V., Dahl-Jensen, D., Johansson, M., Kovacs, K. M., Michel, C., Prowse, T. , Reist, J. D. and Sharp, M. 2011. Ecological implications of changes in the Arctic cryosphere. Ambio, 40: 87-99.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10: 91-164.

Winberg, G. G. 1956. Rate of metabolism and food requirements of Fishes. Belorussian State University Minsk. Translated from Russian by Fish. Res. Bd Can. Transl. Ser. 194: 251 p.

Yaremchuk, G.C.B. 1986. Results of a nine year study (1972–1980) of the sport fishing exploitation of lake trout (*Salvelinus namaycush*) on Great Slave and Great Bear lakes NWT. The nature of the resource and management options. Can. Tech. Rep. Fish. Aquat. Sci. 1436: 89.

Zimmerman, M. S., Krueger C. C. and Eshenroder, R. L. 2006. Phenotypic diversity of lake trout in Great Slave Lake: differences in morphology buoyancy and habitat depth. Trans. Am. Fish. Soc. 135:1056-1067.

Zimmerman, M. S., Schmidt, S.N., Krueger, C. C., Vander Zanden, M. J. and Eshenroder, R. L. 2009. Ontogenetic niche shifts and resource partitioning of lake trout morphotypes. Can. J. Fish Aquat. Sci. 66: 1007-1018.

Table1. List of functional groups and data source for the Great Slave Lake Ecopath model

Functional Group	Parameter	Data source
Lake Trout *Salvelinus namaycush*	Life history parameters and habitat	Falk et al. 1973, Gillman and Roberge 1982, Low et al. 1999
	Biomass/Relative abundance	Indirect method, Roberge et al. 1985
	P/B	Empirical estimation , Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Rawson 1951, Vander Zanden and Rasmussen 1996
	Catch	Read and Taptuna 2001 TEK (unpublised)
Pike *Esox lucius*	Life history parameters and habitat	Roberge et al. 1985, Falk and Gillman 1975
	Biomass	Indirect method, Roberge et al. 1985
	P/B	Empirical estimation , Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Rawson 1951, Little et al. 1998
	Catch	Read and Taptuna 2001, TEK (unpublished)
Inconnu *Stenodus leucichthys*	Life history parameters and habitat	Fuller 1955, Day and Low 1993
	Biomass	Indirect method, Roberge et al. 1985
	P/B	Empirical estimation , Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Rawson 1951, Fuller 1955, Little et al. 1998
	Catch	Read and Taptuna 2001, TEK (unpublished)
Walleye *Sander vitreus*	Life history parameters and habitat	Babaluk et al. 1993
	Biomass	Indirect method, Roberge et al. 1985
	P/B	Empirical estimation , Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Rawson 1951, Little et al. 1998
	Catch	Read and Taptuna 2001, TEK (unpublished)
Burbot *Lota lota*	Life history parameters and habitat	Bond 1974, Roberge et al. 1985, Stewart et al. 1999.
	Biomass	Indirect method, Roberge et al. 1985
	P/B	Empirical estimation , Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Rawson 1951, Little et al. 1998
	Catch	Read and Taptuna 2001, TEK (unpublished)
Ciscoes Mostly *Coregonus artedi*, least cisco *C. sardinella*	Life history parameters and habitat	Bond 1974, Roberge et al. 1985
	Biomass	Indirect method, Roberge et al. 1985
	P/B	Empirical estimation ,Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Rawson 1951, Vander Zanden and Rasmussen 1996
	Catch	Read and Taptuna 2001, TEK (unpublished)
Sculpin Slimy sculpin, *Cottus cognatus*, Spoonhead sculpin *Cottus ricei*, Deepwater sculpin (*Myoxocephalus thompsonii*)	Life history parameters and habitat	Mohar 1985, Richardson et al. 2001, Sheldon 2006, Froese and Pauly 2011,
	Biomass	Estimated by Ecopath model
	P/B	Empirical estimation , Pauly 1980
	Q/B	Empirical estimation , Palomares and Pauly 1998
	Diet	Sheldon 2006, Froese and Pauly 2011,
Lake whitefish *Coregonus clupeaformis*	Life history parameters and habitat	Roberge et al. 1985, Low and Read 1987, Tallman and Friesen 2007

	Biomass	Indirect method, Roberge et al., 1985
	P/B	Roberge et al. 1985, Pauly, 1980
	Q/B	**Empirical estimation** , Palomares and Pauly 1998
	Diet	Rawson 1951, Vander Zanden and Rasmussen 1996, Little et al. 1998
	Catch	Read and Taptuna 2001, TEK (unpublished)
Arctic grayling *Thymallus arcticus*	Life history parameters and habitat	Falk and Gillman 1975
	Biomass	Indirect method, Roberge et al. 1985
	P/B	**Empirical estimation** , Pauly 1980
	Q/B	**Empirical estimation** , Palomares and Pauly 1998
	Diet	Rawson 1951, Stewart et al. 2007a
	Catch	Read and Taptuna 2001, TEK (unpublished)
Round whitefish *Prosopium cylindraceum*	Life history parameters and habitat	Roberge et al. 1985.
	Biomass	Indirect method, Roberge et al. 1985.
	P/B	**Empirical estimation** , Pauly, 1980
	Q/B	**Empirical estimation** , Palomares and Pauly 1998
	Diet	Rawson 1951, Stewart et al. 2007b
	Catch	Read and Taptuna 2001, TEK (unpublished)
Suckers Mostly *Catostomus catostomus*	Life history parameters and habitat	Bond 1974,Stewart et al. 1999
	Biomass	Indirect method, Roberge et al. 1985
	P/B	**Empirical estimation** , Pauly 1980
	Q/B	**Empirical estimation** ,Palomares and Pauly 1998
	Diet	Rawson 1951, Little et al. 1998
	Catch	Read and Taptuna 2001, TEK (unpublished)
Chub Mostly lake chub *Couesius plumbeus*	Life history parameters and habitat	Richardson et al. 2001, Froese and Pauly 2011.
	Biomass	Estimated by Ecopath Model
	P/B	**Empirical estimation** , Pauly 1980
	Q/B	**Empirical estimation** , Palomares and Pauly 1998
	Diet	Scott and Crossman 1985, Richardson et al. 2001, Froese and Pauly 2011
Other fish Ninespine Stickleback (*Pungitius pungitius*), least cisco *C. sardinella*, spottail Shiner (*Notropis hudsonius*), emrald shiner (*Notropis atherinoides)* Trout-perch *(Percopsis omiscomaycus)*	Life history parameters and habitat	Scott and Crossman 1985, Richardson et al. 2001, Randall, and Minns 2000, Froese and Pauly 2011, Golder Associates Ltd. 2010, 2011,
	Biomass	Estimated by Ecopath model
	P/B	**Empirical estimation** , Pauly 1980(mean values)
	Q/B	**Empirical estimation** , Palomares and Pauly 1998 (mean values)
	Diet	Scott and Crossman 1985, Hartman 1992, Froese and Pauly 2011
Mysids *Mysis relicta*	Abundance / Biomass / Habitat	Larkin 1948, Rawson 1953, Muir et al. 2009
	P/B	Waters 1977, Jorgensen 1977, Kitchell et al. 2000
	Q/B	Estimated by Ecopath model
	Diet	Grossnickle 1982; Kitchell et al. 2000
Zooplankton Mostly Copepoda (*Diaptomus sicilis, Diaptomus ashlandi*), Cyclops (*Bicuspidatus thomasi*) and Cladocera (*Daphnia longiremis)*	Abundance / Biomass / Habitat	Muir et al. 2009, Estimated by Ecopath model
	P/B	Waters 1977; Jorgensen 1977
	Q/B	Estimated by Ecopath model
	Diet	Kitchell et al. 2000
Amphipods *Pontoporeia affinis, Gammarus limnaeus*	Abundance / Biomass / Habitat	Larkin 1948, Rawson 1953, Muir et al. 2009, Moore 1977, Moore 1979
	P/B	Waters 1977, Jorgensen 1977, Kitchell et al. 2000
	Q/B	Estimated by Ecopath model

	Diet	Moore1977
Other benthos Chironomidae (mostly *Spaniotoma*), Gastropoda (*Valvata sincera, Gyraulus parvus*), Oligochaeta (*Tubifex*) and Sphaeriidae (*Pisidium conventus, Pisidium subtruncatum*)	Abundance / Biomass / Habitat	Rawson 1953, Muir et al. 2009
	P/B	Waters 1977, Jorgensen 1977, Kitchell et al. 2000
	Q/B	Estimated by Ecopath model
	Diet	Kitchell et al. 2000
Primary Production Mostly phytoplankton	Biomass	Fee et al. 1985
	Production	Fee et al. 1985
Detritus non-living particulate organic material	Biomass	Empirical estimation (Christensen et al. 2005)

Table 2. Balanced parameter estimates for the Great Slave Lake Ecopath model. Bold values were calculated by the Ecopath model.

Group name	Trophic level TL	Biomass (t/km²)	P/B	Q/B	EE	P/Q	Harvest			
							Com.	Sub.	Disc.	Total
Lake trout	**4.1**	0.038	0.140	1.600	**0.605**	**0.088**	0.0028	0.0001	0.0003	0.0029
Pike	**4.0**	0.089	0.530	1.840	**0.182**	**0.288**	0.0053	0.0003	0.0005	0.0056
Inconnu	**4.1**	0.010	0.620	2.100	**0.278**	**0.295**	0.0015	0.0001	0.0002	0.0016
Walleye	**4.0**	**0.007**	0.480	2.400	0.900	**0.200**	0.0006	0.0000	0.0001	0.0006
Burbot	**3.8**	0.132	0.510	5.200	**0.091**	**0.098**	0.0019	0.0001	0.0020	0.0020
Ciscoes	**3.2**	0.258	0.560	2.500	**0.816**	**0.224**	0.0000	0.0001	0.0010	0.0001
Sculpins	**3.1**	**0.223**	0.810	14.700	0.900	**0.055**				
Lake whitefish	**3.0**	0.661	0.650	2.400	0.355	**0.271**	0.0382	0.0019	0.0038	0.0401
Arctic grayling	**3.0**	**0.006**	0.400	2.300	0.900	**0.174**				
Round whitefish	**3.0**	0.008	0.390	2.500	**0.731**	**0.156**				
Suckers	**3.0**	0.250	0.450	5.270	**0.892**	**0.085**	0.0003	0.0000	0.0020	0.0003
Chub	**2.9**	**0.002**	0.900	12.000	0.900	**0.075**				
Other fish	**3.0**	**0.182**	1.150	15.750	0.900	**0.073**				
Mysids	**2.6**	**0.619**	2.000	25.00	0.900	**0.080**				
Zooplankton	**2.1**	**1.465**	13.000	52.00	0.900	0.250				
Amphipods	**2.0**	2.380	2.000	8.000	**0.693**	0.250				
Other benthos	**2.0**	1.670	3.000	12.00	**0.727**	0.250				
Primary Production	**1.0**	8.200	30.800		**0.314**					
Detritus	**1.0**	1.100			**0.175**					

Commercial (Com), Subsistence (Sub), Discard (Disc),

Table 3. Balanced diet matrix for the Great Slave Lake ecosystem Ecopath model showing proportions of each prey in the diet of predators.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Lake trout	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Pike	-	0.01	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Inconnu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Walleye	-	0.01	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Burbot	-	0.01	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Ciscoes	0.50	0.05	0.30	0.05	0.10	-	-	-	-	-	-	-	-	-	-	-	-
7	Sculpin	0.10	-	0.05	-	0.23	-	-	-	-	-	-	-	-	-	-	-	-
8	Lake whitefish	0.09	0.12	0.23	0.05	0.11	-	-	-	-	-	-	-	-	-	-	-	-
9	Arctic grayling	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Round whitefish	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Suckers	-	0.10	0.10	0.10	0.11	-	-	-	-	-	-	-	-	-	-	-	-
12	Chub	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Other fish	0.20	0.55	0.30	0.49	0.10	-	-	-	-	-	-	-	-	-	-	-	-
14	Mysids	0.03	-	-	-	0.23	0.28	0.17	0.01	-	-	-	-	0.07	-	-	-	-
15	Zooplankton	-	-	-	-	-	0.60	0.07	-	-	-	0.05	-	0.39	0.50	0.10	-	-
16	Amphipods	0.04	0.05	0.00	0.10	0.06	0.01	0.44	0.37	0.42	0.02	0.48	-	0.20	-	-	-	-
17	Other benthos	0.01	0.05	0.02	0.10	0.06	0.10	0.33	0.61	0.21	0.98	0.45	0.70	0.30	-	-	-	-
18	Primary Production	-	-	-	-	-	-	-	-	-	-	0.01	0.10	0.04	0.30	0.90	0.10	0.20
19	Detritus	-	-	-	-	-	-	-	-	-	-	0.01	-	-	0.20	-	0.90	0.80
20	Import	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00
21	Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 4. Trophic transfer matrix of the Great Slave Lake ecosystem Ecopath model showing the distribution of absolute flows ($t.km^{-2}.yr^{-1}$) by groups and trophic levels.

	Trophic level (TL)				
Group Name	I	II	III	IV	V
Lake trout	0.00	0.00	0.00	0.05	0.01
Pike	0.00	0.00	0.02	0.14	0.01
Inconnu	0.00	0.00	0.00	0.02	0.00
Walleye	0.00	0.00	0.00	0.01	0.00
Burbot	0.00	0.00	0.16	0.50	0.03
Ciscoes	0.00	0.00	0.55	0.09	0.00
Sculpins	0.00	0.00	3.01	0.27	0.00
Lake whitefish	0.00	0.00	1.58	0.01	0.00
Arctic grayling	0.00	0.00	0.01	0.00	0.00
Round whitefish	0.00	0.00	0.02	0.00	0.00
Suckers	0.00	0.03	1.24	0.00	0.00
Chub	0.00	0.00	0.02	0.00	0.00
Other fish	0.00	0.12	2.63	0.10	0.00
Mysids	0.00	7.74	7.74	0.00	0.00
Zooplankton	0.00	76.12	0.00	0.00	0.00
Amphipods	0.00	19.04	0.00	0.00	0.00
Other benthos	0.00	20.04	0.00	0.00	0.00
Primary Production	252.60	0.00	0.00	0.00	0.00
Detritus	207.00	0.00	0.00	0.00	0.00
Total	459.50	123.10	16.99	1.20	0.04

Table 5. Transfer efficiency at various TLs showing the contribution of detritus and primary production to the Great Slave Lake trophic network.

Source \ Trophic level	II	III	IV	V
Producer	13.8	7.5	5.6	2.3
Detritus	16.8	6.9	2	4.7
All flows	14.7	7.3	4.4	2.4
Proportion of total flow originating from detritus: 0.42				
Transfer efficiencies (calculated as geometric mean for TL II-IV)				
				From primary producers: 8.3%
				From detritus: 6.2%
				Total: 7.8%

Table 6: A summary of metrics and indices for structural properties of the Great Slave Lake ecosystem

Parameter	**Value**	**Units**
Sum of all consumption	141.32	$t.km^{-2}.year^{-1}$
Sum of all exports	170.77	$t.km^{-2}.year^{-1}$
Sum of all respiratory flows	81.81	$t.km^{-2}.year^{-1}$
Sum of all flows into detritus	206.98	$t.km^{-2}.year^{-1}$
Total system throughput	600.88	$t.km^{-2}.year^{-1}$
Sum of all production	283.81	$t.km^{-2}.year^{-1}$
Mean trophic level of the catch	3.24	
Gross efficiency (catch/net pp.)	0.00025	
Calculated total net primary production	252.56	$t.km^{-2}.year^{-1}$
Total primary production/total respiration	3.09	
Net system production	170.75	$t.km^{-2}.year^{-1}$
Total primary production/total biomass	15.60	
Total biomass/total throughput	0.03	
Total biomass (excluding detritus)	16.19	$t.km^{-2}$
Total catch	0.06	$t.km^{-2}.year^{-1}$
Connectance Index	0.25	
System Omnivory Index	0.08	

Table 7. Totals of flux indices for the Great Slave Lake ecosystem model.

	Ascendency		Overhead		Capacity	
Source	(flowbits)	(%)	(flowbits)	(%)	(flowbits)	(%)
Import	0.20	0.00	0.10	0.00	0.20	0.00
Internal flow	306.20	15.80	907.40	46.80	1213.60	62.60
Export	262.20	13.50	48.70	2.50	310.80	16.00
Respiration	171.50	8.80	242.60	12.50	414.10	21.40
Total	740.10	38.20	1198.70	61.80	1938.80	100.00

Table 8. Primary Production Required (PPR) for consumption and harvest of functional groups in the Great Slave Lake ecosystem

Group name	TL	Consumption			Harvest		
		PPR/consumption	PPR/PP (%)	PPR/u.biom	PPR/catch	PPR/PP (%)	PPR/u.catch
Lake trout	4.07	84.87	1.12	0.30	969.94	0.68	2.11
Pike	3.96	197.01	7.02	0.79	683.95	0.91	1.49
Inconnu	4.06	84.66	0.39	0.39	286.76	0.11	0.62
Walleye	3.95	519.63	2.00	2.71	2598.13	0.39	5.65
Burbot	3.83	89.29	13.34	1.01	910.43	0.79	1.98
Ciscoes	3.23	12.92	1.81	0.07	57.66	0.01	0.13
Sculpins	3.10	10.39	7.42	0.33	22.08	0.21	0.05
Lake whitefish	3.01	5.98	2.06	0.03	22.22	0.23	0.05
Arctic grayling	3.00	3.58	0.01	0.02			
Round whitefish	3.00	5.50	0.02	0.03			
Suckers	2.98	5.46	1.57	0.06	63.96	0.03	0.14
Chub	2.88	3.95	0.02	0.10			
Other fish	3.04	6.87	4.28	0.24			
Mysids	2.56	2.50	8.42	0.14			
Zooplankton	2.11	0.90	14.92	0.10			
Amphipods	2.00	1.00	4.14	0.02			
Other benthos	2.00	1.00	4.36	0.03			
Total					228.28	3.13	0.5

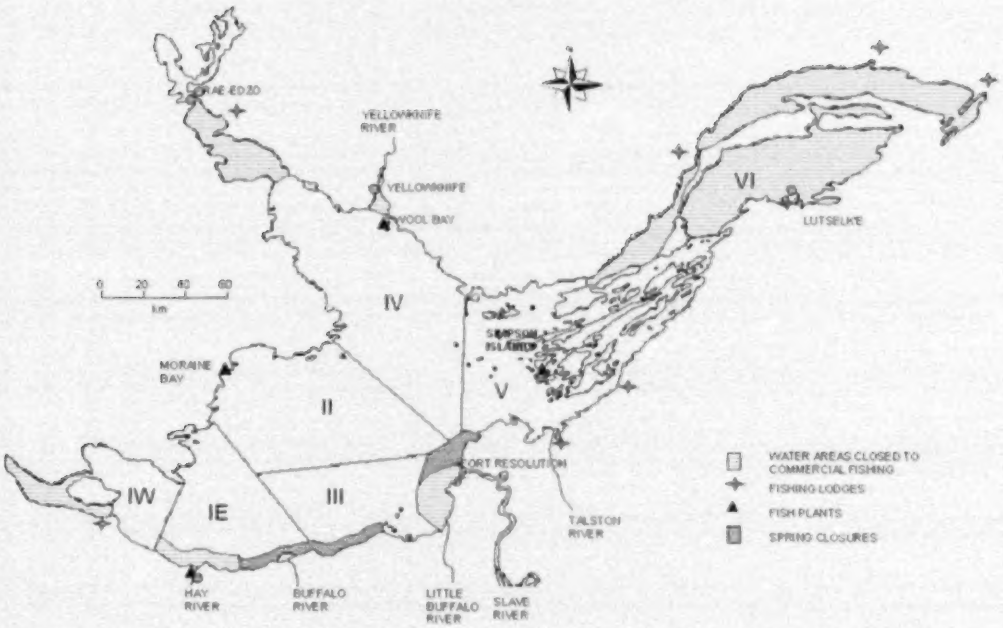

Figure 1. Map of the Great Slave Lake showing the management areas and areas closed to commercial fishing.

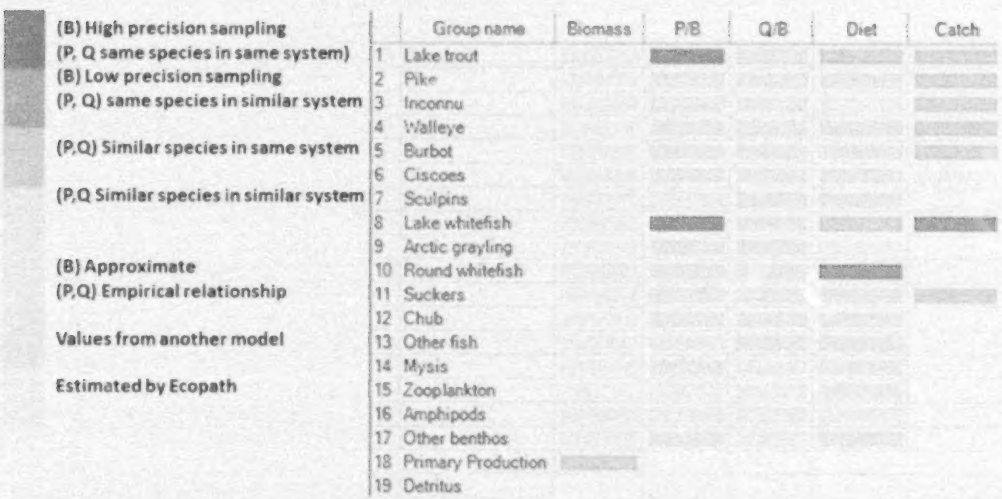

Figure 2. Pedigree index of data used for the Great Slave Lake Ecopath model. Colors in the legend describe the data origin and quality.

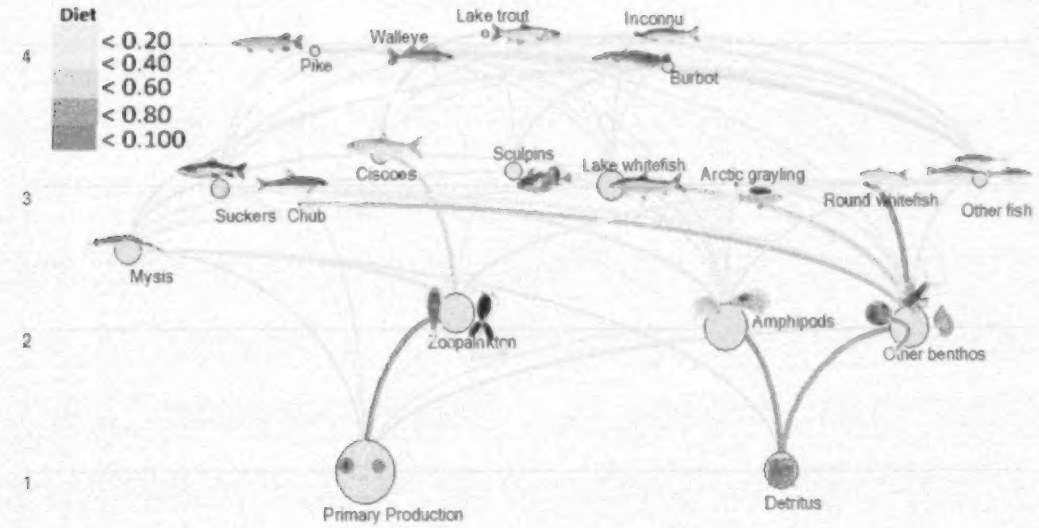

Figure 3. The Ecopath outputs based on the Great Slave Lake food web conceptualization. Each functional group is shown as a circle and its size is approximately proportional to its biomass. Colour of the lines illustrate the magnitude of the flow. The horizontal lines demonstrates trophic levels of each functional group.

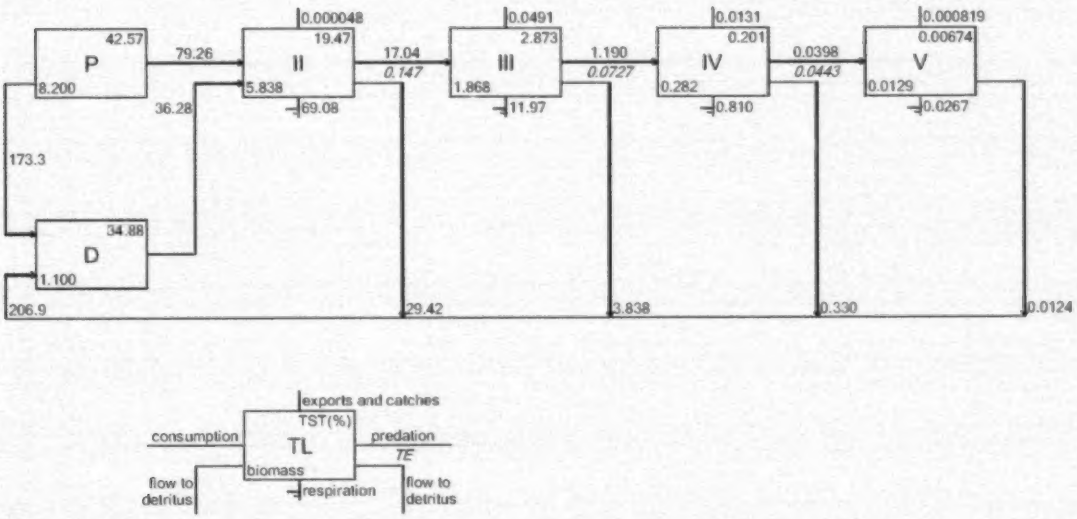

Figure 4. Lindeman spine of the Great Slave Lake ecosystem showing aggregation of flows into a concatenated chain of transfers through trophic levels. Values are described in the legend.

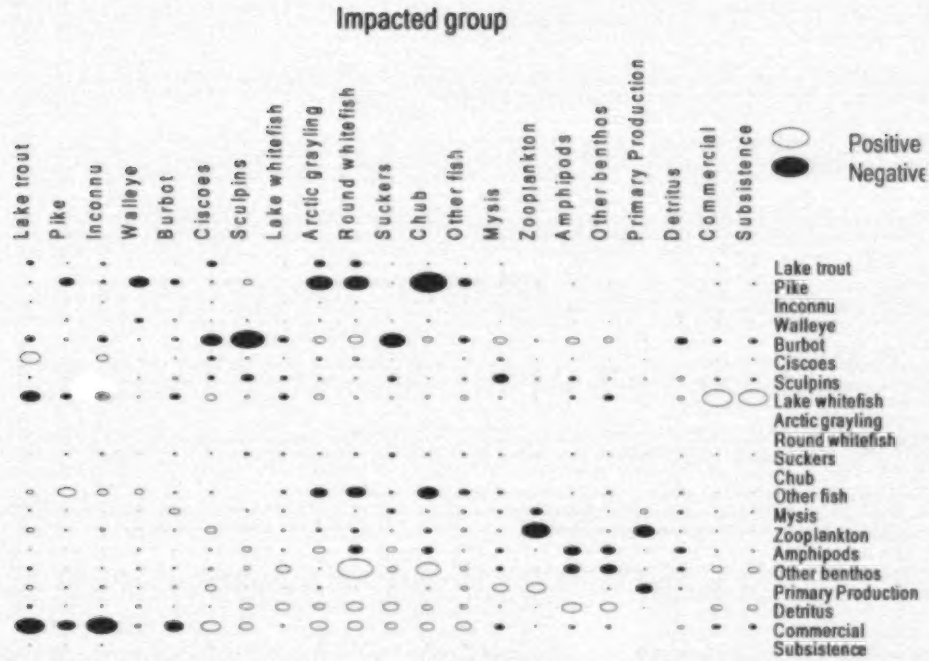

Figure 5. Mixed trophic impact of the Great Slave Lake ecosystem. White circles represent a positive impact and black circles indicate a negative impact. The sizes of circles are proportional to the degree of the impacts.

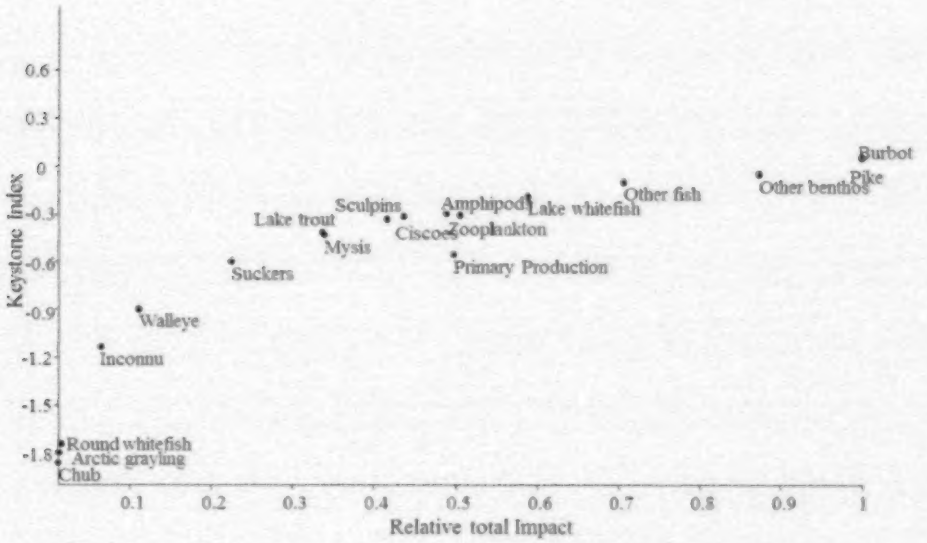

Figure: Keystoneness of different functional groups in Great Slave Lake. Keystone groups are those with a higher Keystone Index and a higher relative total impact.

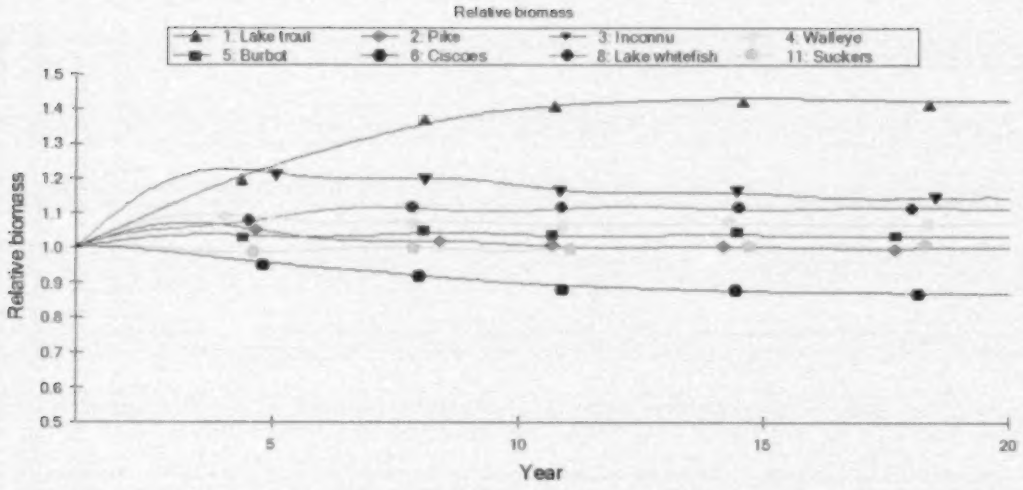

Figure 7. Predicted relative change in biomass of fished species in Great Slave Lake in 20-years period by reducing the fishing to 25%.

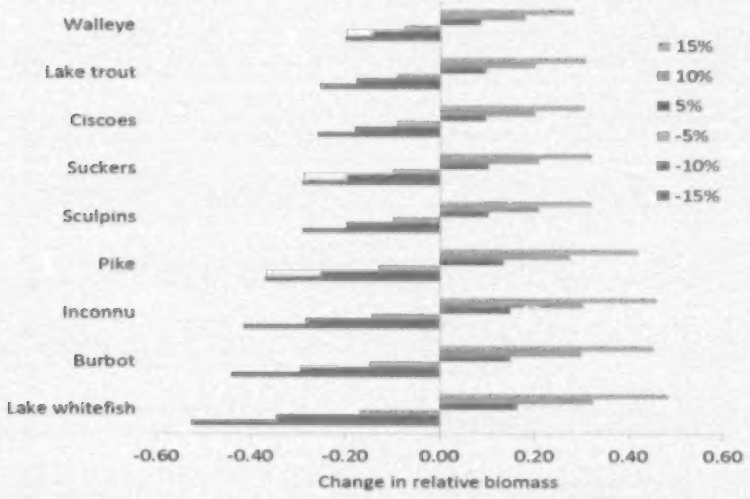

Figure 8. The relative change in biomass of functional groups in the Great Slave Lake ecosystem after imposing a -15% to +15% changes in the primary production over a 50-year period. Results show the comparatively greater increase in relative biomass of lake whitefish, burbot and inconnu.